

REVIEWS

Juvenile Forms and Flower Maturity*

During a residence in West Australia, Diels found the relation between vegetative growth and generative maturity subject to change and became acquainted with the conditions that correspond to the phases of these changes. He found a large number of cases in which flowering occurred in juvenile forms. A search in the literature showed that this "abnormality" is far-reaching and calculated "to throw light upon a new side of form-diversity in the plant kingdom."

His book does not attempt a complete enumeration of such cases but endeavors, by typical examples, to illustrate the many-sidedness of the question.

The first chapter, entitled, "*Die Bedingtheit der Blütenreife*," discusses various explanations that have been offered as to the conditions of flowering. The older theory of Moebius (1847) was that every plant species which, through heredity, possesses fixed characters, produces flowers at a definite age or phase of its development. Diels, however, agrees with the view more recently expressed by Klebs (1904), "that flower formation by phanerogamous plants presents the same problem in principle as does the sexual reproduction of algae, or the fruiting of the higher fungi. * * * "I hold," says Klebs, "that a quantitative increase of the concentration of organic material with all its physical and chemical consequences plays an important rôle in the transition from growth to reproduction." "The external circumstances," says Diels; "either inhibit or accelerate, according as they interfere with or favor, the internal conditions necessary to flowering." Experimental researches on the problem have been few, but Diels believes that a new review of the cases hitherto published of flowering in a very early developmental stage will not be without its value.

Chapter II, "*Das Verhältniss der Blütenreife zur vegetativen Entwicklung in seiner Wandelbarkeit*," gives citations from literature, presenting cases illustrating the relation of flowering to

* Diels, L. Jugendformen und Blütenreife im Pflanzenreich. Pp. 1-130. *f.* 1-30. Berlin: Gebrüder Borntraeger. 1906.

vegetative development in its changes. The cases cited indicate that there is a "vast independence of generative maturity and vegetative growth. Of course a definite 'nutrition-minimum' is absolutely necessary. Beyond this, the way for generative maturity, flowering (*Die Blütenreife*), arises independently. Every favoring constellation is able to induce it, even though vegetative development be insignificant, and though the age be juvenile. Practically, all cases of 'early blooming,' or on the other hand of 'nanism,' signify how flowering is favored 'by dryness or by the disturbance of the nutrition conducive to growth.'"

In Chapter III, "*Helikomorphie und Blütenreife bei heteroblastischen Pflanzen*," the author refers to Goebel's classification of development into "heteroblastic," where the differences between the configuration of the plant at different stages in its vegetative development are very small, and "homoblastic," where these differences are large. Goebel, in his "Organography," has already pointed out that no sharp line can be drawn between homoblasts and heteroblasts. Juvenile forms (*Jugendformen*) and subsequent forms (*Folgeformen*) have been recognized. Diels proposes to apply to both the general term "helikomorph." "I call a form a 'helikomorph,' " he says, "which appears at a definite phase of vegetative development, that is, at a definite (relative) age (Gr. *ἡλικία* = age)." The term signifies, in general, the vegetative configuration dependent upon the phase or age.

Helikomorphs are classed as: 1. Heteroblasts with arrested primary leaves; 2. Heteroblasts with arrested subsequent leaves (*Folgeblättern*); 3. Heteroblasts with helikomorphs of indeterminate characters. The greater portion of the book (pp. 23-108) is occupied with illustrations of the various classes, under the subheads, (a) cases conditioned by external conditions (*exogener Bedingtheit*), including seasonal dimorphism; (b) cases whose conditions are unknown.

The phylogenetic significance of helikomorphs is discussed in Chapter IV. "After the attainment of a certain minimum of vegetative preparation, flowering can occur in very diverse phases of development and bring about the termination of vegetative unfolding."

“When this happens within heteroblastic species or genera, then there follows a corresponding difference in the entire morphological expression of the individual forms. We rank these forms as individual variations if observation or experiment demonstrates their connection with the ‘normal.’” (*Limosella* presents an example of this.) “We call them species if such experience is wanting. But often these standards are uncertain.” One recalls very distinctly an example in the case of *Campanula rotundifolia*. Of their early-blooming form, Goebel rightly says, they would, “in another botanical district and occurring in larger number, be considered without hesitation as a different species from *Campanula rotundifolia*. There is not the slightest doubt but that in fact many so-called ‘species’ bear the same relation to other species as the Schleissheim *Campanula* (p. 86) does to the ‘normal’ plants, that they also stand mutually in the relation of helikomorphic forms.”

“Often phase-forms prove themselves to be ‘epharmons’ (*Epharmosen*). Theoretically they must quite frequently begin as such, because the relation between vegetative growth and reproduction is so labile, and because external conditions are in continual change.”

“In each case these epharmonic phase-forms will endure as long as the determinative conditions remain nearly similar. They may, indeed, exist under circumstances of very long duration. And thereby they acquire the possibility of becoming fixed through heredity and of losing more and more the primary strict dependence upon external circumstances.”

“This case has found realization in many similar forms. * * * The Australian acacias form their phyllodes even in our houses. I have seen examples of *Eucalyptus Risdoni* that escape from culture of European gardens and bear inflorescences as in their home locality.”

“Heredity has also been demonstrated in the case of the ‘seasonal dimorphic’ species. Von Wettstein has cultivated *Euphrasia Rostkoviana* and *E. montana* through three years in the botanical garden at Prague under entirely similar external conditions. The two plants proved themselves fully constant in

all their characters, in their whole behavior." (Ber. Deutsch. Bot. Ges. 13: 307. 1895.) "Now if Von Wettstein's plausible assumptions concerning the established causes of this dimorphism are correct, then even the state of heredity is here a relatively very young epharmon (*Epharmon*): for only since the development of an alpine habit (*Alpenwirtschaft*) through regular mowing would the effective forces have been in action. If only a phylogenetically considered short period suffices in this case to fix the form as hereditary, by how much more would nature itself, which operates over such immeasurably long periods, be in a condition to do it. Through heredity numerous helikomorphic structures obtain that independence which establishes new phyletic courses for their posterity. They become, then, 'phylembryos' of new developmental courses. Their leaf-form, fixed in a definite direction, undergoes either epharmonic or autogenous variations, a new strain is developed out of the former phase-form of the old stock."

Chapter V treats of similar phenomena in the animal kingdom, and Chapter VI is a résumé of the preceding chapters. The following is a free translation of Chapter VI, with omission of the examples cited :

"The generative maturity of plants is not unchangeably bound up with a definite stage of vegetative development. Of course it presumes a certain minimum of previous vegetative work ; if this is exceeded, however, there follows *a broad zone of variation for the appearance of the flowers*. The regulation of this variation takes place by means of complex and diverse conditions. *External circumstances* have an important share in it, in the case of cryptogams (Klebs) as well as in the case of flowering plants. Of this we know but little ; but it is manifestly evident that *dryness and a qualitative variation of nutrition favor flowering, opposite conditions are unfavorable*.

"The vegetative ontogeny of plants is consummated through the coöperation of autogenous and external (*exogener*) factors. The ground work comprises diverse potentialities. Thus it postulates no rigid configuration. At first the environment is rather 'the determining factor as to which of the various possible

developmental forms becomes realized.' *This regulation by means of the environment is clearly realized in the case of heteroblastic ontogenesis.*

"As in the case of flowering, the insight into the associations which we have hitherto obtained is rather limited. But we see that the organization of subsequent leaves (*Folgeblätter*) becomes more abundant if heat and moisture are increased. And we recognize a restriction in this respect by shortening the growth period, by dryness, and by a lowering of the temperature.

"Thus ontogeny varies with the quality and degree of external factors. The finished figure of the organism is the product of vegetative ontogeny and of flower-maturity: and *both factors are variable.*

"And furthermore their variability is not of the same kind nor similarly ordered. Of course the vegetative form-development ceases for the most part with flowering; but that is a stage, however, where the two courses of development, the vegetative and the generative, are indissolubly connected. Otherwise they are free and independent of each other. Their relation is capable of every variation. The leaf-succession in its phase (helikomorphie) varies after its own fashion. Flowering varies in its own way.

"In this combination of two variable factors into the unity of the flowering form, lies a powerful impetus to the increase of form-diversity in the plant kingdom. For the circumstances that help to regulate the leaf-succession and flower-maturity vary with the change of climate in time and place. In their ultimate effects they produce the geographically local races (*Arten*) and in the course of time favor the development of new species. Their product attains to heritability, and thereby new strains with new possibilities become established.

"In this relation of consecutive vegetative stages and flowering, it is expressed with clear emphasis how endlessly variable form is in the plant kingdom. Even the few external factors that we perceive, produce an interminable maze of possibilities. We are led indeed to the confession to which Klebs was led in another connection: 'The typical or customary development

signifies only a small, limited portion of the complement of possible forms.' Such utterances, often enough already expressed, are, notwithstanding the clear conception of species of our day, still far remote from fruitful effect."

The book, on the whole, is very suggestive along several lines. In the first place, it shows how possible it is to arrive at new and possibly important results merely by a reëxamination and reconsideration of the rich material already collected both in herbaria and in published literature. In the second place, it emphasizes the great desirability of collecting and preserving in herbaria unusual or abnormal forms, as well as so-called "typical" specimens. In the third place, it gives emphasis to the value and absolute need of experimental pedigree culture, at least as ancillary to morphological and systematic work, for the reason that origin of species is more a physiological than a morphological problem, and can never be solved by employing alone the methods of comparative anatomy.

Finally, added importance is attached to the "heliokomorphs" as material upon which selection may act in the development of new groups of the rank of species. In this connection, also, the question of the heritability of acquired characters is forced once more to the front.

The burden of proof still lies with those who deny that species of plants as well as of animals, are formed in more than one way. As has been recently often stated, it is only by a combination of ecological and physiological studies that we may hope for a proper interpretation of the facts of comparative anatomy and ultimately of the method of organic evolution.

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Postelsia, reviewed in *TORREYA* 6: 250. December, 1906, may be obtained from Professor Josephine E. Tilden, University of Minnesota, Minneapolis, Minn.